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Phylogeny and Evolutionary History of Old World Suboscine Birds (Aves: Eurylaimides)

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ABSTRACT

Molecular and morphological data were used to derive a phylogenetic hypothesis for the Eurylaimides, an Old World bird group now known to be distributed pantropically, and to investigate the evolution and biogeography of the group. Phylogenetic results indicated that the Eurylaimides consist of two monophyletic groups, the pittas (Pittidae) and the broadbills (Eurylaimidae sensu lato), and that the broadbills consist of two highly divergent clades, one containing the sister genera *Smithornis* and *Calyptomena*, the other containing *Pseudocalyptomena graueri*, *Sapayoa aenigma*, the asity genera *Philepitta* and *Neodrepanis*, and five Asian genera. Our results indicate that over a ~10 million year time span in the early Tertiary, the Eurylaimides came to inhabit widely disjunct tropical regions and evolved disparate morphology, diet, and breeding behavior. Biogeographically, although a southern origin for the lineage is likely, time estimates for major lineage splitting do not correspond to Gondwanan vicariance events, and the biogeographic history of the crown clade is better explained by Laurasian climatic and geological processes. In particular, the timing and phylogenetic pattern suggest a likely Laurasian origin for the sole New World representative of the group, *Sapayoa aenigma*.

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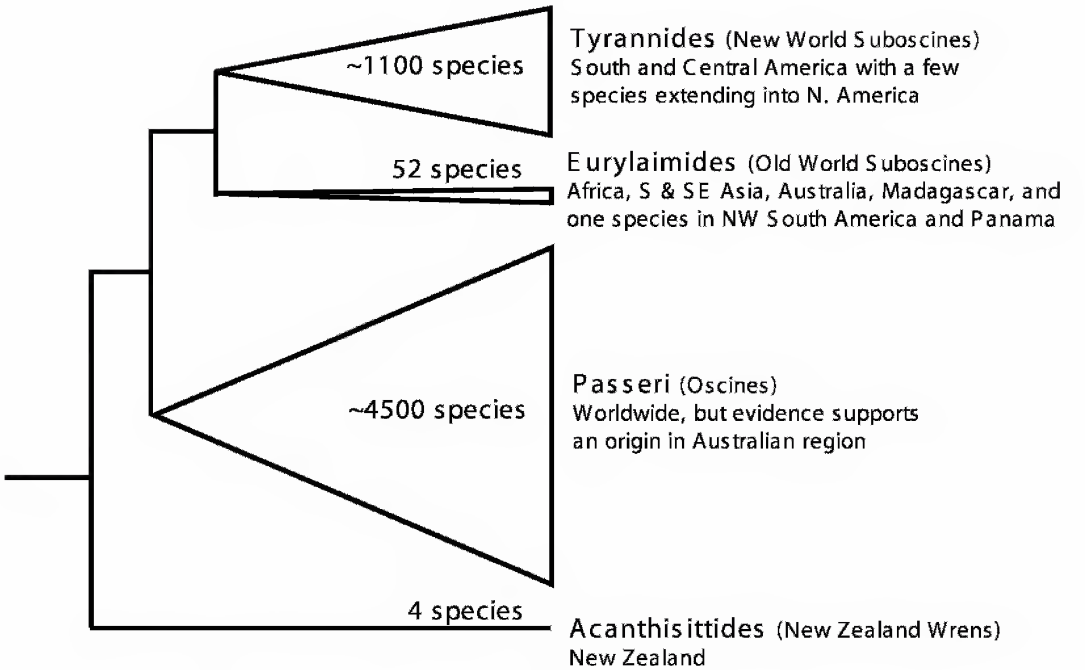
~1100 species
Tyrannides (New World Suboscines)
South and Central America with a few
species extending into N. America
52 species
Eurylaimides (Old World Suboscines)
Africa, S & SE Asia, Australia, Madagascar, and
one species in NW South America and Panama
~4500 species
Passeri (Oscines)
Worldwide, but evidence supports
an origin in Australian region
4 species
Acanthisittides (New Zealand Wrens)
New Zealand

Fig. 1. Summary of passerine bird distribution and basal relationships (from Barker et al., 2002, 2004; Ericson et al., 2002).

INTRODUCTION

Recent molecular studies have dramatically improved our understanding of phylogenetic relationships within the passerines, or perching birds (e.g., Barker et al., 2002, 2004, and Ericson et al., 2002), a large clade containing roughly half of extant bird species (fig. 1). These phylogenetic advances bolstered the biogeographic hypothesis (e.g., Cracraft, 1974, 2001) that passerines originated on the Gondwanan supercontinent in the Late Cretaceous, and subsequently radiated in New Zealand (Acanthisittidae), South America (Tyrannides), and Australia (Passeri). Today, the Tyrannides and Acanthisittidae occur largely within their inferred area of origin, but the Passeri (oscine passerines) have colonized much of the globe via multiple dispersal events out of Australasia (Barker et al., 2004).

Largely unresolved are the relationships and biogeographic history of the fourth major lineage of passerines, the Eurylaimides or Old World suboscines, which have traditionally consisted of the pittas, broadbills, and asities. This group, although small in species numbers, includes taxa with highly divergent morphologies, nest architectures, and feeding strategies. Pittas (genus *Pitta*) are distributed in Asia (22 species), Australasia (9 species), and Africa (2 species), and are secretive terrestrial insectivores that build domed nests on the ground (Erritzoe, 2003). Broadbills are primarily Asian (six genera, 11 species) but also contain two African genera (4 species); these arboreal insectivores and frugivores build pendulous nests from the tips of long branches, and many species have a remarkably wide bill (Bruce, 2003). The frugivorous and nectarivorous asities (2 genera, 4 species) are Malagasy endemics, with one genus convergent on the nectarivorous morphotype of hummingbirds (Trochilidae) and sunbirds (Nectariniidae). Recent evidence that the Eurylaimides also include a single Neotropical species, *Sapayoa aenigma*, a small olive-colored frugivore/insectivore found in the Chocó region of Panama, western Colombia, and Ecuador (Fjeldsa et al., 2003; Chesser, 2004), greatly expands the geographic scope of the group, yielding a pantropical distribution.

The Eurylaimides are an exemplary group for examining how a taxon became pantropical. The clade is part of a large radiation having Gondwanan origins (fig. 1: Barker et al., 2002, 2004; Ericson et al., 2002, 2003), inasmuch as its nearest outgroups (fig. 1) originated in South America (Tyrannides), Australia (Passeri), and New Zealand (Acanthisittides). In contrast, although sparse, the fossil record of Old World suboscines is restricted to Europe (Ballman, 1969; Mourer-Chauvire, 1995), pointing to a Laurasian history. Recent phylogenetic studies have suggested that they arose or diversified on the Indian subcontinent (e.g., Barker et al., 2004; Fjeldsa et al., 2003). With indications of Gondwanan, Laurasian, and Indian Ocean histories, the Eurylaimides offer a unique opportunity to examine the relative influence of each region on the biogeographic history of a pantropical radiation.

Using nuclear DNA sequences from all genera, along with a suite of morphological characters, we reconstruct the evolutionary history of the Eurylaimides, with the following objectives: (1) to develop a well-supported phylogenetic hypothesis for the group, including placement of the Neotropical species *Sapayoa aenigma*; (2) to examine the evolution of diet within the group in light of new ideas about phylogenetic relationships; (3) to estimate a timescale for the diversification of the Eurylaimides; and (4) to reconstruct their biogeographic history. By expanding taxon and character sampling over previous studies (e.g., Raikow, 1987; Prum, 1993; Fjeldsa et al., 2003) we are able to clarify relationships and improve estimates of the timing and pattern of differentiation in this widespread tropical group.

METHODS

Taxon and Character Sampling

Ingroup sampling (see appendix 1) included all genera of Old World (OW) suboscines (11 genera, 23 species), as well as a New World representative, *Sapayoa aenigma*, recently shown to be part of the OW radiation (Fjeldsa et al., 2003; Chesser, 2004). Outgroup taxa were drawn from other passerine groups (5 species) and nonpasserines (1 species). DNA was extracted, amplified, and sequenced using standard protocols (see Barker et al., 2004; Moyle, 2005). Two exons of the nuclear recombination-activating gene (RAG-1 and RAG-2) and β-fibrinogen intron 5 (Fib5), totaling just over 4.6 kb, were sequenced for taxa represented by fresh tissue. Primers for all amplifications and sequencing were from previous studies (Groth and Barrowclough, 1999; Barker et al., 2004; Driskell and Christidis, 2004). DNA from four species (including three monotypic genera) could be obtained only from toe-pads clipped from museum skins. Using taxon-specific primers (table 1) and amplifying short fragments of DNA, we sequenced a large portion of the RAG-1 exon for these species.

Syringeal, osteological, and myological characters were taken from Raikow (1987) and Prum (1993) and used in combined phylogenetic analyses; characters from Prum (1993) were newly coded for *Sapayoa aenigma* and *Corydon sumatranus* (appendix 2).

TABLE 1
RAG-1 Primers Used to Amplify and Sequence Short Fragments of DNA Extracted from Museum Study Skins

Arrows indicate forward and reverse primers. Primers are listed in pairs (i.e., R101 and R104 used together, R103 and R106 used together, etc.).

Name	Sequence (5′ to 3′)
R102← (paired with R13[a])	AAATGAAACTCCACAGATGCG
R101→	CAATAGAGCTCATCAGAACAAT
R104←	TACTGAATTTTCTATGGATAA
R103→	TTGATACTATCCATCCCACTCG
R106←	TCTTTCATTAAATTTTTGTTGTTT
R105→	AACGTGTGAAGACCATTGTGG
R108←	AGCAAGGATACCAGCAGGAGGG
R107→	ACATGCAGACACTTGTTTTGCAG
R110←	AGAGCTCTCTATCTTTCATCTCC
R109→	AAAGGAATGTGATGAAGAGATC
R112←	CTCATCTGCTTGTCTGTGTTCAT
R111→	AAGGCTGTATGCATGACTTTG
R114←	ATAACCTGGTAGGAGGGCTTTC
R113→	ACAGATCTTCCAGCCTTTGC
R116←	AGATTTTTTGCTTTCATGCCTTC
R115→	GATGCAGCCTTGGTTTGTGCC
R118←	TCTGAATTGGGCTTTACTTCTTC
R117→	TTTCACAGTTATGAACATTGC
R120←	CACAAGTTTCTCATCATATCC

[a] Groth and Barrowclough, 1999.

Phylogenetic Analyses

Maximum parsimony (MP) analysis, with TBR branch-swapping, was performed with PAUP* 4.0b10 (Swofford, 2002) and equal weighting of all characters. Branch support was assessed with 1000 nonparametric bootstrap replicates. For likelihood analyses, Modeltest 3.7 (Posada and Crandall, 1998) was employed to determine the model of evolution and parameter estimates. Model parameters and phylogenetic relationships were also estimated in a Bayesian framework with MrBayes 3.1.1 (Ronquist and Huelsenbeck, 2003). A general time-reversible model framework, with gamma-distributed rates among sites and invariant sites (GTR + G + I), was used in all Bayesian analyses. We ran four Markov chains for 10 million generations as well as two shorter runs of 2 million generations. The shorter runs were used to examine whether our analyses were stuck in local optima (Huelsenbeck and Bollback, 2001) and to evaluate stationarity, the condition in which trees are sampled according to their posterior probabilities. Stationarity was judged by visually inspecting plots of likelihood scores. All samples prior to reaching stationarity were discarded. Markov chains were sampled every 1000 or 500 generations, depending on the length of the run, yielding 10,000 and 4000 point estimates of parameters, respectively. These subsamples, minus the burn-in generations, were used to create consensus trees. We took a cautious approach and removed more samples than indicated by visual inspection of the likelihood plots to ensure that burn-in runs were not included in our consensus trees (Leaché and Reeder 2002). Thus, although stationarity appeared to occur by 200,000 generations in all Bayesian analyses, we removed 1 million generations before compiling consensus trees.

Three datasets were available for analysis. First, all of the data were combined (nuclear exons, nuclear intron, and morphology) for parsimony analysis with equal weighting of all characters and 1000 bootstrap replicates. This combined analysis utilized unordered characters and used two New World suboscines (*Furnarius rufus* and *Tyrannus tyrannus*) as outgroup taxa because they were primitive for the morphological characters analyzed (Prum, 1993). Results of these analyses were used to examine character evolution within the group (see below). Although the combined data matrix contained the most available characters, it also contained a large amount of missing data because Fib5, RAG-2, or certain morphological data were not available for all taxa. The second data matrix consisted of full or partial nuclear exon data, which were available for all taxa. The full complement of parsimony, likelihood, and Bayesian analyses was performed on this matrix, and the results were the basis for analysis of ancestral areas and divergence times (see below). Third, a reduced taxon set was represented by RAG-1, RAG-2, and Fib5 data (those taxa extracted from skins or that did not amplify were omitted). Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed on this data set. Node support was estimated by bootstrapping (1000 MP replicates, 100 ML replicates).

Evolution of Diet

Analyses of the evolution of diet in the Eurylaimides were conducted using the program MacClade 4.06 (Maddison and Maddison, 2003). Diet was mapped onto the combined morphological/molecular tree for Eurylaimides, using parsimony reconstruction of unordered characters. Ancestral dietary state for the Eurylaimides was determined using outgroup analysis of diets in other major groups of passerines (as in fig. 1, but with the large groups Tyrannides and Passeri further divided into their constituent sister groups: Tyranni and Furnarii, and Menurae and Passeres, respectively). Outgroups were coded "insectivorous" if the group is predominantly insectivorous (i.e., Acanthisittidae, Furnarii, Menurae) or "polymorphic" if the group contains both predominantly insectivorous and predominantly frugivorous, granivorous, or nectarivorous taxa (i.e., Tyranni, Passeres). For the one major passerine group (Menurae) not sampled as an outgroup in this study, topological position was based on the passerine phylogeny corroborated by several recent studies (Barker et al., 2002, 2004; Ericson et al., 2002). Separate analyses were conducted

using each combination of character states in the case of polymorphic groups.

Diet within Eurylaimides was coded in accordance with the predominant dietary mode of each species, based on data in Prum (1993), Lambert and Woodcock (1996), Bruce (2003), Hawkins (2003), Erritzoe (2003), and references cited in these sources. Diets consisting primarily of insects and other invertebrates, supplemented in some taxa with occasional small vertebrates or fruit, were coded "insectivorous", and diets consisting primarily of fruit, supplemented with occasional insects or nectar, were coded "frugivorous". Diets consisting primarily of nectar but that also include insects were coded as "nectarivorous". Dietary data for unsampled species of Eurylaimides were checked to ensure that diets of species not included in the phylogeny were similar to those of sampled congeners.

Ancestral Areas and Divergence Times

We used two parsimony-based methods, weighted ancestral area analysis (WAAA; Hausdorf, 1998) and dispersal-vicariance analysis (DIVA; Ronquist, 1997), to estimate the ancestral area for OW suboscines. Analyses were conducted using the combined molecular /morphological tree, although we also generated a conservative estimate of the ancestral distribution by using all three potential arrangements of the major clades in DIVA analyses (see results for details). Species were coded geographically by broad regions: Asia, Africa, Madagascar, Australia, and New World. In DIVA, vicariance is assumed, and inferred dispersal events are assigned a cost. Long distance or stepping-stone dispersal likely contributed to the current distribution of the Eurylaimides, therefore an a priori assumption of vicariance is not appropriate. To account for this, DIVA contains a useful feature in which the maximum number of areas in the ancestral distribution can be limited. This is particularly appropriate given the areas inhabited by the Eurylaimides and the time frame in question. The regions (South America, Australia, Africa, Madagascar, and India/Asia) have experienced a complex history due to plate tectonics over the last 150 million years. Africa has not been in contact with other Gondwanan landmasses since ~100 Ma (Mascle et al., 1988), well before the time frame inferred for diversification of passerine birds. Madagascar and India separated by 84 Ma (Plummer and Belle, 1995), and South America and Australia were connected via Antarctica only until about 55–60 Ma (Woodburn and Case, 1996). Thus, not only was the ancestral area of the Eurylaimides likely confined to no more than two regions, the ancestral area of any subclade (e.g., pittas) was probably confined to no more than two areas. Because of these geographic restrictions, we conservatively limited the maximum number of regions in the ancestral area to three.

Weighted Ancestral Areas Analysis (WAAA) uses reversible parsimony to estimate the ancestral area for a group of organisms. It differs from Ronquist's (1994) reversible-parsimony method in that it measures the difference in losses and gains of states (areas), weighted by their position in the tree. Thus, state changes along distal branches are down-weighted relative to basal state changes. Compared to DIVA, WAAA is less sensitive to the effects of large unit areas (regions), in which allopatric speciation and subsequent sympatry may occur (Hausdorf, 1998). The large number of sympatric species of broadbills and pittas in Southeast Asia indicates that this may be a concern in the OW suboscines.

We tested the molecular data for clocklike evolution with a likelihood-ratio (LR) test (Felsenstein, 1981). LR tests determined that the data did not adhere to a molecular clock, so we used penalized likelihood (PL; Sanderson, 2002) in the program r8s (Sanderson, 2003) to transform the maximum likelihood tree into an ultrametric topology. The smoothing parameter for PL was chosen by a cross-validation procedure (Sanderson, 2003). Node heights were transformed from units of molecular change into units of time by calibration to a geological vicariance event. There is strong support for the basal relationships of Passeriformes and for their Gondwanan origin (Barker et al., 2002, 2004; Ericson et al., 2002). The basal branch in the passerines includes the New Zealand wrens

(*Acanthisitta*); thus we used the opening between the greater New Zealand continental block and West Antarctica, taken here to be 82–90 Ma (Yan and Kroenke, 1993; Gaina et al., 1998), as our geological calibration (see Cracraft, 2001; Ericson et al., 2002; Barker et al., 2004 for additional discussion). A molecular rate calibration for the avian cytochrome *b* gene is consistent with this geological calibration (Barker et al., 2004). The standard deviation of age estimates was estimated by bootstrapping the data set 100 times and repeating the penalized likelihood and calibration procedure.

RESULTS

Sequence Attributes

The nuclear exon data matrix included 24 ingroup taxa and 4039 characters (2887 RAG-1 and 1152 RAG-2). The matrix contained 564 parsimony informative characters (384 RAG-1, 180 RAG-2), and both genes had base composition that was skewed (RAG-1: A = 0.32, C = 0.20, G = 0.24, T = 0.24; RAG-2: A = 0.30, C = 0.21, G = 0.22, T = 0.27) but homogeneous across taxa (chi-square test implemented in PAUP*) and typical of these genes in other birds (e.g., Groth and Barrowclough, 1999; Barker et al., 2004; Moyle, 2005). The nuclear intron data matrix included 21 taxa (17 ingroup and four outgroup taxa) and 590 characters. The matrix contained 160 parsimony informative characters, and base composition was skewed (A = 0.31, C = 0.16, G = 0.21, T = 0.32) but homogeneous across taxa (chi-square test implemented in PAUP*).

All sequences were aligned by eye, which was fairly straightforward for two reasons: First, indels were infrequent enough that they generally did not overlap, allowing homologous indels to be easily identified. Second, the nucleotide sequences themselves were not highly diverged, which allowed straightforward alignment and default placement of indels. The RAG-1 and RAG-2 matrices contained a single instance of length variation: an autapomorphic one-codon deletion in one of the outgroup taxa (*Tyrannus*). The aligned intron matrix contained several inferred indels. When compared to the tree resulting from analysis of all three genes (fig. 4), most indels shared by multiple taxa can be explained by single insertions or deletions. The indels are found in: the entire ingroup (10 bp, 21 bp); all of the pittas (8 bp, 1 bp, 2 bp); *Eurylaimus* and *Serilophus* (1 bp, 7 bp, 19 bp); *Philepitta* and *Neodrepanis* (3 bp); *Pitta sordida*, *Pitta Iris*, and *Pitta versicolor* (21 bp); and clades A and B (1 bp). One insertion could not be reconstructed as a single event. A 2-bp insertion (of an "AT" repeat) was found in clade A (*Calyptomena* and *Smithornis*) and *Neodrepanis*. No analysis found a close relationship between *Neodrepanis* and clade A, so this shared insertion is inferred to be homoplastic.

Phylogenetic Relationships

Phylogenetic analysis of the three data matrices yielded strong support for monophyly of the Eurylaimides (figs. 2, 3, 4), including the Neotropical species *Sapayoa aenigma*. Three main clades, one of pittas and two of broadbills, were recovered. One broadbill clade (A) contained the African genus *Smithornis* and the Asian genus *Calyptomena*. The second broadbill clade (B) consisted of *Sapayoa aenigma*, the two Malagasy genera (*Philepitta* and *Neodrepanis*), five Asian genera (*Psarisomus*, *Serilophus*, *Cymbirhynchus*, *Corydon*, and *Eurylaimus*), and the monotypic African genus *Pseudocalyptomena*. The third clade (C) contained all *Pitta* species sampled: seven from Asia, two from Australia, and one from Africa.

The two broadbill clades were sister taxa (i.e., broadbills were monophyletic) in analyses of the combined molecular/morphological dataset (fig. 2) and of the molecular dataset including the RAG genes and Fib5 (fig. 4). Relationships among the three main clades of pittas and broadbills were unresolved when the exon data were analyzed separately (fig. 3). Within broadbill clade B, the Asian genera (*Psarisomus*, *Serilophus*, *Cymbirhynchus*, *Corydon*, and *Eurylaimus*) formed a monophyletic group and were sister to the African genus *Pseudocalyptomena*. The asities, genera *Philepitta* and *Neodrepanis* (often considered the separate family Philepittidae), were sister to the Asian + *Pseudocalyptomena*

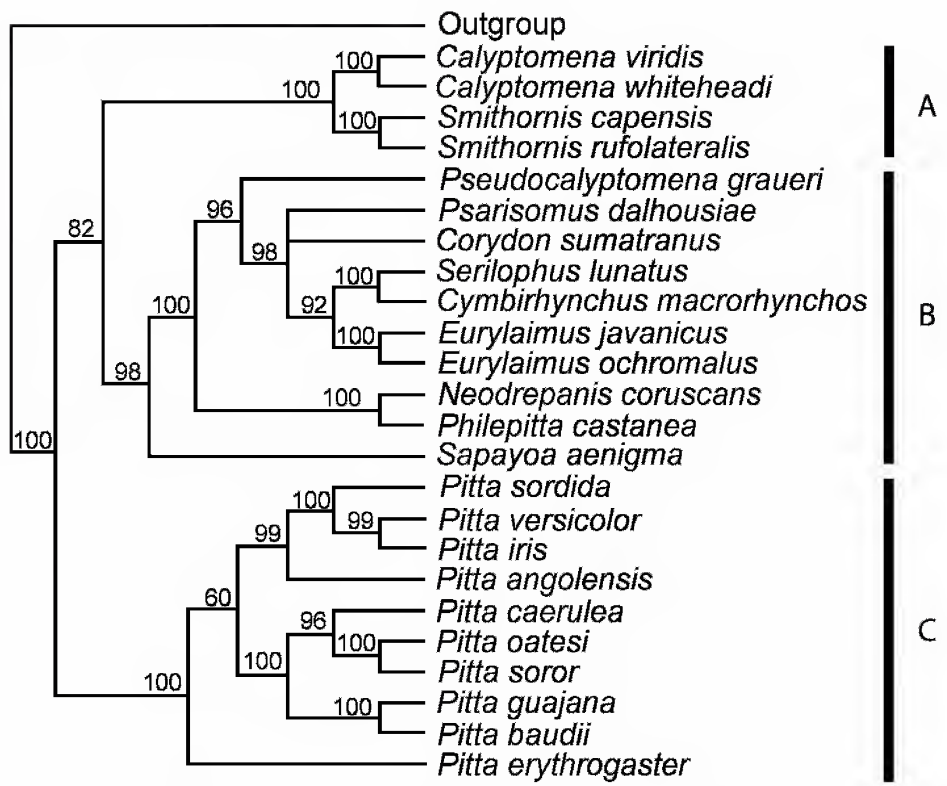

Fig. 2. Strict consensus of four maximum parsimony (MP) trees from analysis of combined RAG-1, RAG-2, Fib5, and morphological characters. Numbers by nodes indicate MP bootstrap support.

clade, and the Neotropical taxon *Sapayoa aenigma* was sister to the Asian + *Pseudocalyptomena* + asity clade.

In all analyses, most nodes received high support, with bootstrap proportions above 80% and Bayesian posterior probability above 0.95. Parsimony analysis of the combined molecular/morphological data matrix yielded a tree (fig. 2) with all but two nodes receiving bootstrap support above 90%. The two nodes with lower support (< 50%), one that places *Pitta erythrogaster* within a subclade of pittas and one that unites *Psarisomus* and *Corydon* as sister genera, are not well resolved in any of the analyses (see figs. 3, 4) but do not affect higher-level inferences of biogeography or character evolution.

Evolution of Diet

Most species of Eurylaimides (i.e., all species in the genera *Smithornis*, *Psarisomus*, *Corydon*, *Cymbirhynchus*, *Eurylaimus*, *Sapayoa*, and *Pitta*) were determined to be insectivorous; *Calyptomena*, *Pseudocalyptomena*, and *Philepitta* species were found to be frugivorous and the two species of *Neodrepanis* nectarivorous. These character states agree with previous codings (Prum, 1993), although *Sapayoa* was not included in the prior analysis. Although some general sources (Hilty and Brown, 1986; Snow, 2004) state that *Sapayoa aenigma* eats fruit and insects, we were unable to find documentation of substantial frugivory in this species. Indeed, the only published data of which we are aware, Christian's (2001) observations both of foraging adults and of food delivered to nestlings, indicated that only insects were taken. Although foraging in this instance may have been modified to provision young with a protein-rich insectivorous diet, stomachs of three birds collected at a different time of year (LSUMZ 108443, 108444, 108918) also contained only insect remains. The broad bill of *Sapayoa aenigma*, reminiscent of those of flat-

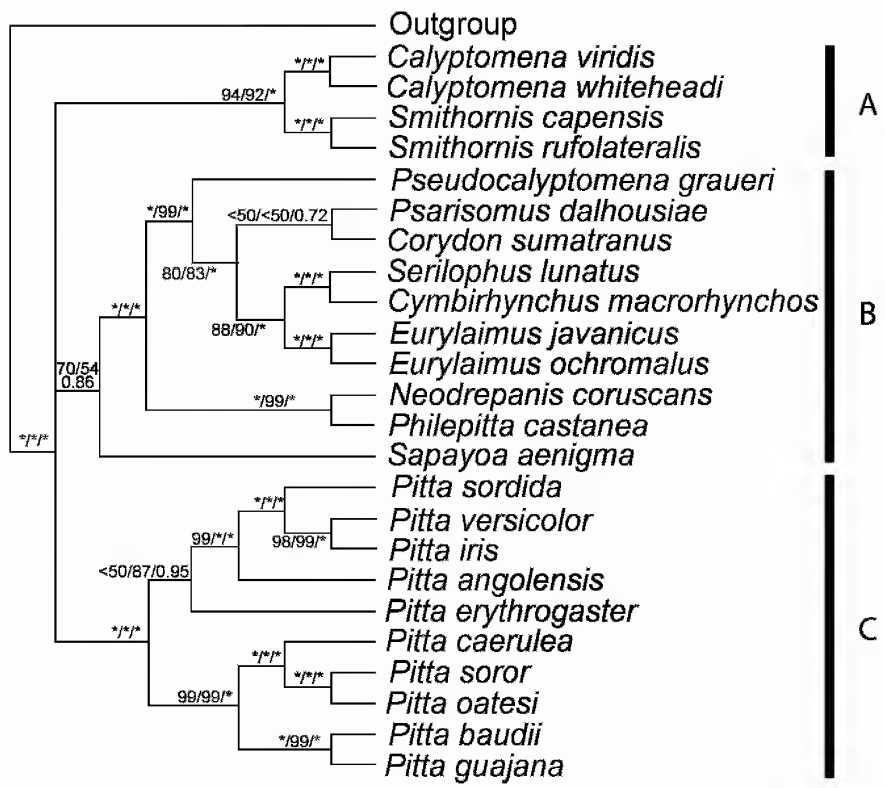

Fig. 3. Maximum likelihood (ML) estimate of phylogeny from sequences of the RAG-1 and RAG-2 nuclear exons. Numbers by nodes indicate MP bootstrap support/ ML bootstrap support/ Bayesian posterior probability. Asterisks (*) indicate bootstrap support of 100% or posterior probability of 1.0.

billed flycatchers, its rictal bristles, and its habit of joining insectivorous understory mixed-species flocks (Ridgely and Tudor, 1994), further suggest a predominantly insectivorous diet.

All analyses of character evolution indicated that the Eurylaimides evolved from an insectivorous ancestor (fig. 5). Reconstruction of ancestral states indicated that frugivory has evolved two or three times within the group, once in the genus *Calyptomena* and either once or twice within the clade of broadbills containing *Pseudocalyptomena* and the Malagasy and Asian broadbills, and that nectarivory has evolved once (fig. 5). Independent development of frugivory in *Pseudocalyptomena* and *Philepitta*, with retention of insectivory in all genera except *Neodrepanis*, is equally parsimonious to development of frugivory in the nearest common ancestor of *Pseudocalyptomena* and *Philepitta* with subsequent loss of frugivory as the predominant diet in the Asian broadbills and in *Neodrepanis*.

Biogeography of the Eurylaimides: Pattern and Timing

Despite the presence of taxa from multiple continents in each clade, WAAA reconstructed Asia as the best estimate of the ancestral area (table 2). Asia's probability index was 1.30, whereas all other areas had probability indices less than 0.40 (Australasia, 0.29; Madagascar, 0.125; New World, 0.165; Africa, 0.39). Probability indices are not on an absolute scale and thus cannot be directly interpreted as a probability of being the ancestral area. However, in this instance Asia's probability index was a clear outlier. Its probability index was more than three times that of any other area, and all other areas' values were clustered within a small range (0.125 to 0.39). DIVA also returned Asia alone as the ancestral area of the Eurylaimides based on the topology shown in figure 2. Asia was likewise reconstructed as

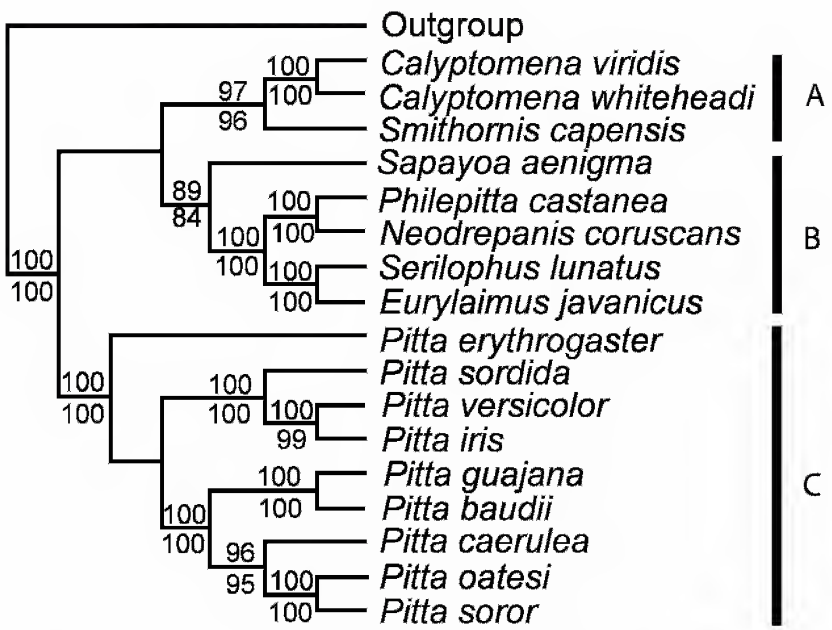

Fig. 4. Single MP tree from analysis of RAG-1, RAG-2, and Fib5 data. Numbers above branches indicate MP bootstrap support, numbers below branches are ML bootstrap support.

the ancestral area for alternate topology (B(A+C)), and for topology (A(B+C)) DIVA reconstructed either Asia or Asia + Africa as the ancestral area (see table 3 for details).

The DNA sequence data failed a likelihood-ratio test for clocklike evolution ($p < 0.001$), so the maximum likelihood tree was transformed into an ultrametric tree with penalized likelihood. A calibration range of 82–90 mya at the origin of *Acanthisitta* yielded age estimates (fig. 6) and standard deviations (SD) for nodes of interest (table 4). The origin of the Eurylaimides stem lineage (fig. 6, node 1) was estimated at 70.2 Ma (1.7 SD). The pitta and two broadbill lineages diverged (node 2) well after the K/T boundary (55.6 Ma). Soon after this initial differentiation into pitta and broadbill clades, *Sapayoa* diverged from its Old World sister taxa (52.5 Ma). Nodes separating African, Asian, and Malagasy clades cluster between 46.4 Ma and 34.7 Ma.

DISCUSSION

Analysis of molecular and morphological data for all genera of OW suboscines provided a well-resolved phylogenetic hypothesis for the group. In particular, our data provided support for several relationships vital for interpreting biogeographic history and character evolution in OW suboscines: (1) monophyly of broadbills, including the asities and *Sapayoa*, with respect to pittas; (2) placement of *Sapayoa* as sister to one of the major clades of broadbills (clade B); and (3) placement of *Pseudocalyptomena* as sister to the group of Asian broadbills within clade B. Below we compare this phylogeny to previous phylogenetic hypotheses for the group and discuss its ramifications for interpreting the evolution of life history traits and biogeographic history.

Comparison to Previous Phylogenetic Hypotheses

Three character-based reconstructions of OW suboscine phylogeny are available for comparison, two based on morphology (Raikow, 1987; Prum, 1993) and one on DNA sequences (Fjeldsa et al., 2003). The most meaningful comparisons are between our study and those of Prum (1993) and Fjeldsa et al. (2003), because Prum's (1993) morphological study included, in addition to new

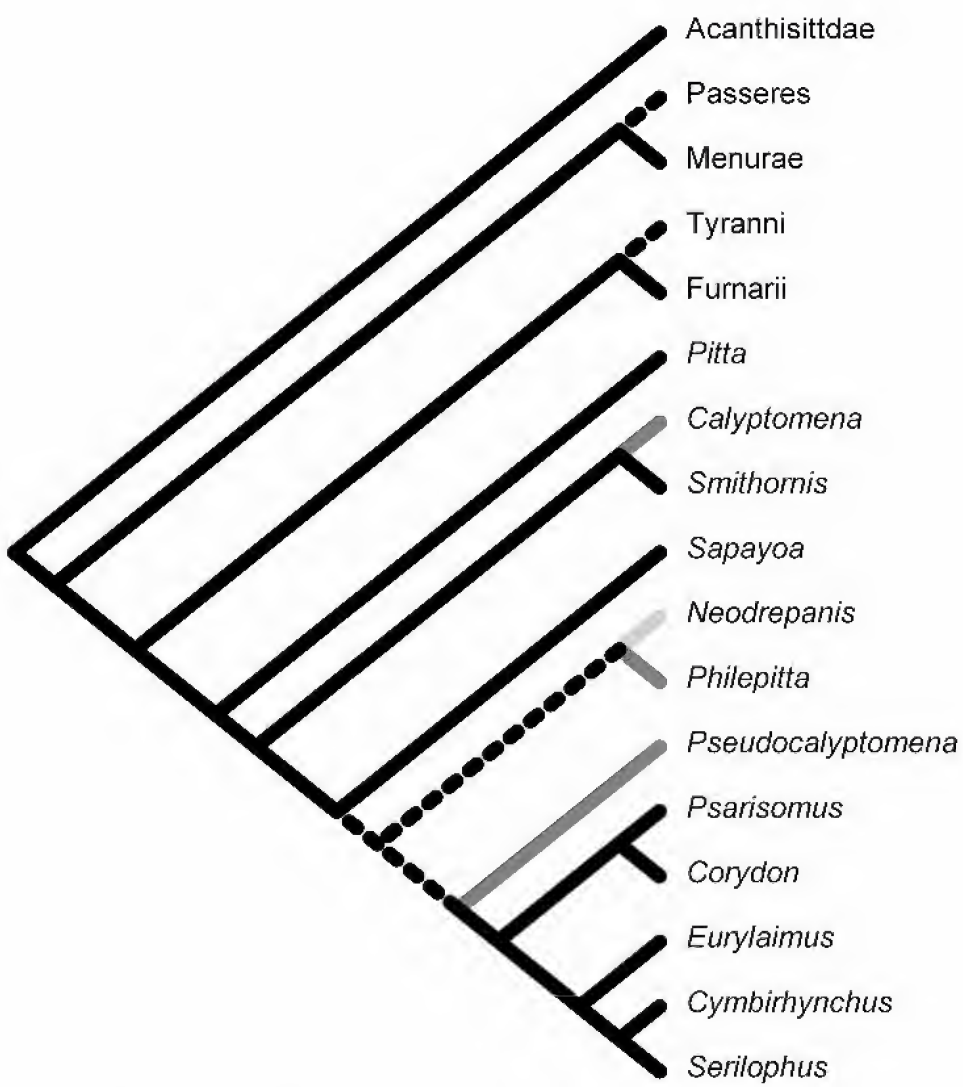

Fig. 5. Parsimonious reconstruction of the evolution of diet in the Eurylaimides. Key: black branches, insectivorous; dark gray branches, frugivorous; light gray branches, nectivorous; and dotted branches, polymorphic/equivocal.

syringeal characters, all informative characters from Raikow's (1987) previous analysis. Fjeldsa et al. (2003) focused on the relationships of *Sapayoa* and sampled a number of OW suboscine taxa, providing several points of comparison with our results.

Pittas, broadbills, and asities were traditionally considered to constitute separate families (Pittidae, Eurylaimidae, and Philepittidae, respectively), and Raikow's (1987) study of hind-limb myology concluded that each family was monophyletic and that the Eurylaimidae and Philepittidae were sister groups. Prum (1993), however, concluded that the Eurylaimidae were monophyletic only if the asities were included (i.e., that the Eurylaimidae were paraphyletic with respect to the Philepittidae). His results indicated that the traditional Eurylaimidae consisted of four groups with successively more-distant sister relationships to the asities: *Pseudocalyptomena* (sister to the Philepittidae), all Asian genera except *Calyptomena* (sister to *Pseudocalyptomena* + Philepittidae), *Calyptomena* (sis-

TABLE 2
Weighted Ancestral Area Analysis (Hausdorf, 1998) for the Old World Suboscines
Distribution for each taxon is given in appendix 1. Characters were mapped in MacClade 4.0 (Maddison and Maddison, 2003) with the ACCTRAN option. GSW = weighted gain steps, LSW = weighted loss steps, PI = probability index.

Region	GSW	LSW	PI
New World	0.33	2.0	0.165
Africa	0.78	2.0	0.39
Asia (with Philippines)	1.73	1.33	1.30
Madagascar	0.25	2.0	0.125
Australasia (to Sulawesi)	0.5	1.75	0.29

ter to all the foregoing taxa), and *Smithornis* (sister to all other broadbills and asities).

Our results are similar to Prum's phylogeny in several respects, most notably the paraphyly of the traditional family Eurylaimidae with respect to the asities. However, our phylogeny differs from that of Prum (1993) in two important points. First, *Calyptomena* and *Smithornis* are sister taxa in our phylogeny, whereas in Prum's tree they are successive sister groups to the other broadbills. Secondly, *Pseudocalyptomena* is sister to the large group of Asian broadbills (*Psarisomus*, *Corydon*, *Serilophus*, *Cymbirhynchus*, and *Eurylaimus*) in our phylogeny, rather than sister to the asities.

Recognition of a *Smithornis-Calyptomena* clade is also supported by a nest-architecture synapomorphy. Prum (1993) previously proposed that the construction of a hanging globular nest was a synapomorphy of the broadbills. In *Smithornis* and *Calyptomena* the main globular nest hangs close to the branch from which the nest is suspended, and the entrance into the nest chamber is immediately below the branch on the upper half of the globe (Bruce, 2003). In all other broadbills, including *Sapayoa* and the asities, the main globular mass of the nest is suspended 10–30 cm below the branch, and the entrance is in the side of the mass (Christian, 2001; Bruce, 2003; Hawkins, 2003). Although it may require new analyses of nest-construction methods in a diversity of broadbills to confirm whether one nest type may have evolved from the other, these two types of nest hanging nest provide unordered behavioral synapomorphies for the basal clades of broadbills.

TABLE 3
Dispersal Vicariance Analysis (Ronquist, 1997) Results for the Eurylaimides
Distribution for each taxon is given in appendix 1. A maximum of three regions was allowed at any node (see text for details). Lettered clades refer to figures 2–4.

Basal topology	Ancestral area
1. *Pitta* basal, (C(A+B))	Asia
2. *Calyptomena* & *Smithornis* basal, (A(B+C))	Asia, or Asia/Africa
3. *Sapayoa* clade basal, (B(A+C))	Asia

TABLE 4
Age Estimates for Nodes of Interest from Penalized Likelihood and a Calibration Range of 82–90 Ma for Divergence of *Acanthisitta*
Node numbers refer to figure 4.

Node[a]	Description	Age (Ma) estimate (SD)[a]
1	Stem of OW suboscine lineage	70.2 (1.6)
2	Diversification of pittas and broadbills	55.6 (1.9)
3	*Sapayoa* splits from broadbills	52.5 (2.2)
4	*Calyptomena*/*Smithornis* split	46.4 (3.0)
5	Origin of asity lineage	41.2 (2.5)
6	*Pseudocalyptomena*	34.7 (3.2)
7	Diversification of Asian broadbills	24.7 (2.3)
8	Diversification of pittas	23.6 (1.8)
9	Origin of African pittas	16.2 (1.6)
10	Origin of Australian pittas	9.0 (1.3)

[a] SD = Standard Deviation from results of 100 bootstrap replicates.

The molecular study of Fjeldsa et al. (2003) indicated that OW suboscines consisted of three major clades consistent with those recovered in this study. However, in their phylogeny the two broadbill clades were not sister groups; that is, the Eurylaimidae were found to be paraphyletic with respect to the Pittidae. While our data concur regarding the distinctiveness of the three lineages, we found no support for paraphyly of the Eurylaimidae sensu lato. Rather, two of our analyses indicated that broadbills are monophyletic, and the other suggested that the three clades formed an unresolved basal polytomy.

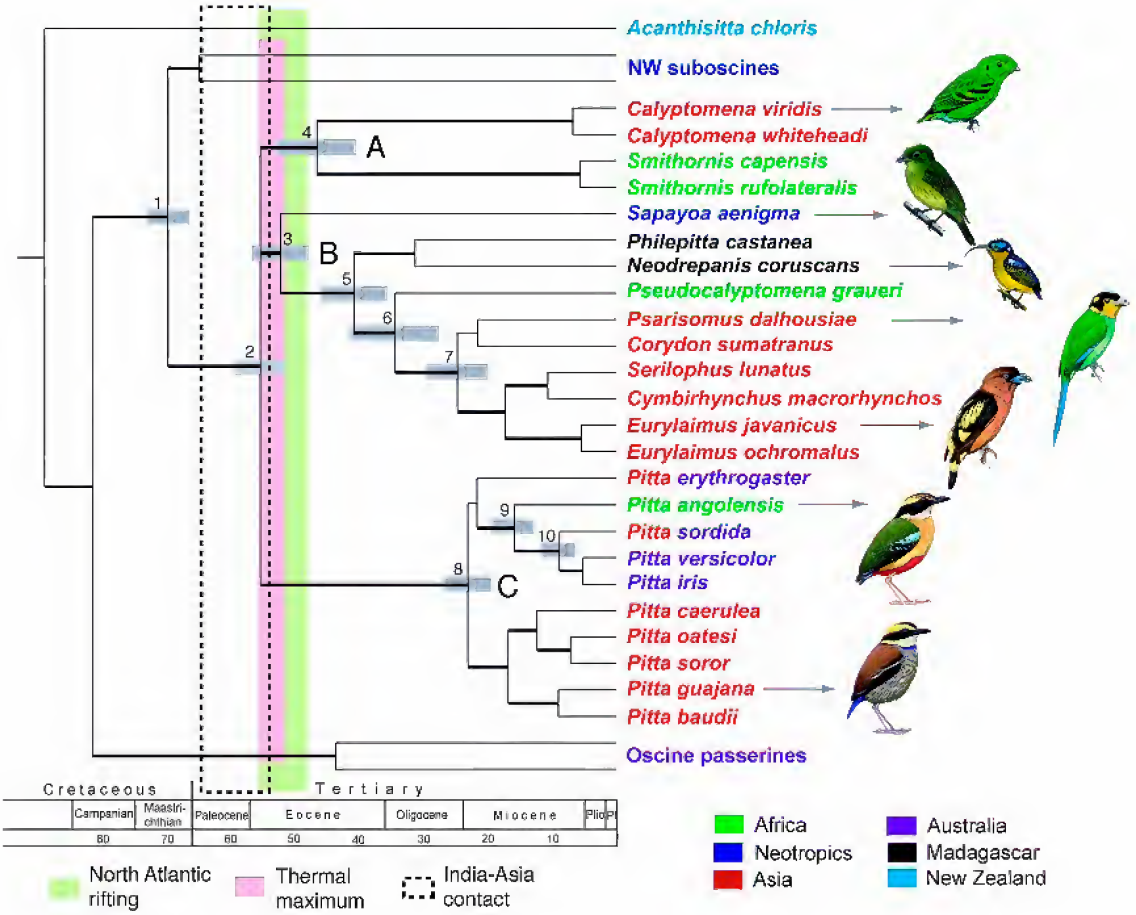

Fig. 6. Diversification of Old World suboscines. Maximum likelihood estimate of phylogeny from RAG-1 and RAG-2 combined data set with thickened branches supported by parsimony bootstrap proportions above 80 and Bayesian posterior probability greater than 0.95 (see figs. 2, 3 for all support values). Date estimates derived with penalized likelihood (Sanderson, 2003) and a calibration of 90–82 Ma between *Acanthisitta* and all other passerines. Horizontal gray bars on nodes indicate ±2 standard deviations of age estimates from bootstrap analysis. The two multicolored species names indicate that the taxon is found in more than one region. Bird images of pittas (C. Rose), broadbills (I. Lewington), asities (J. Cox) and *Sapayoa* (J. Wilczur) are from *Handbook of the Birds of the World*, Vols. 8 and 9, copyright Lynx Ediciones (Josep del Hoyo).

Fjeldsa et al. (2003) were also the first to attempt to place the New World species *Sapayoa aenigma* among the OW suboscines, and they considered *Sapayoa* sister to *Smithornis*/*Calyptomena*, although this result received low branch support. Our analyses supported a sister relationship between *Sapayoa* and a diverse clade of broadbills and asities (clade B), often with high branch support (figs. 2, 4). Independent support for this relationship, although not mentioned by Fjeldsa et al. (2003), is found in their myoglobin intron data. According to their published alignment (EMBL ALIGN_000569), *Sapayoa*, *Philepitta*, *Cymbirhynchus*, *Serilophus*, *Eurylaimus*, and *Psarisomus* share a 2 bp deletion (bases 595 and 596) relative to the other two clades in the Eurylaimides and to the outgroups. The different placement and weak support in Fjeldsa et al. (2003) may simply be due to sparser taxon and character sampling.

All recent phylogenies (Raikow 1987, Prum 1993, Fjeldsa et al. 2003) recovered a clade of

closely related Asian broadbills (*Serilophus*, *Eurylaimus*, and *Cymbirhynchus*), and Prum (1993) suggested that *Corydon* was also a member of this group. Our results corroborate this suggestion and provide strong support for the five Asian genera as a clade. This clade is sister to the monotypic African endemic *Pseudocalyptomena graueri*, as supported both by our combined molecular/morphological data (fig. 2) and by the nuclear exon data alone (fig. 3).

Evolution of Diet

Our analyses indicate that frugivory has evolved two or three times within the Eurylaimides (fig. 5), once in the genus *Calyptomena* and once or twice in the other major broadbill clade. Prum's (1993) analysis, conducted using his morphology-based phylogeny, indicated that frugivory evolved once or twice within the Eurylaimides. According to Prum's (1993) morphological analysis, the insectivorous genus *Smithornis* was sister to all other broadbills. Frugivory evolved either in the ancestor to the remaining broadbills and was subsequently lost in the Asian genera other than *Calyptomena* and in *Neodrepanis*, or independently in *Calyptomena* and in the ancestor to *Pseudocalyptomena* and the asities (sister taxa in Prum's phylogeny) and was subsequently lost in *Neodrepanis*. Prum (1993) argued that independent origins of frugivory in *Calyptomena* and in the *Pseudocalyptomena*/asity ancestor were more likely than a single origin of frugivory with two subsequent losses, in part because of a lack of evidence of homology between the frugivory of *Calyptomena* and that of *Pseudocalyptomena* and *Philepitta*. Although our phylogeny and dietary reconstructions differ, our data support the contention that frugivory in *Calyptomena* evolved independently and is therefore nonhomologous with frugivory in other broadbill genera (fig. 5). In addition, it has been suggested that frugivory in *Calyptomena* species differs qualitatively from that in *Pseudocalyptomena graueri* in that the latter is more omnivorous whereas *Calyptomena* species are true specialist frugivores (Bruce, 2003).

Our phylogeny differs from that of Prum (1993) in that the asities are sister to a clade containing *Pseudocalyptomena* and the insectivorous Asian broadbills rather than sister to *Pseudocalyptomena*; therefore the origin of frugivory in *Pseudocalyptomena* and in the asities bears reexamination. Although the independent development of frugivory in *Pseudocalyptomena* and *Philepitta*, with subsequent loss in *Neodrepanis*, is equally parsimonious to development of frugivory in the nearest common ancestor of *Pseudocalyptomena* and *Philepitta*, with subsequent loss of frugivory in the insectivorous Asian broadbills and in *Neodrepanis*, we suggest that independent development is more likely for two reasons: First, the brush-tipped tongue of *Neodrepanis*, thought to be an adaptation to nectarivory, is also present in *Philepitta* (Lambert and Woodcock, 1996), suggesting that the ancestor of the asities may have been highly nectarivorous and that the frugivory of *Philepitta* evolved via a different pathway than that of *Pseudocalyptomena*. Secondly, as argued by Prum (1993), it may be more likely that the digestive specializations that accompany frugivorous diets would have evolved twice rather than to have undergone two reversals.

Origin of the Eurylaimides and the Role of India

Phylogeny, distribution, and divergence time estimates for passerines as a whole support an origin on the southern continents in the Late Cretaceous (Cracraft, 2001; Barker et al., 2002, 2004; Ericson et al., 2002). Date estimates derived in this study, employing the same methods and vicariance event used to date the passerine radiation (Barker et al., 2004), indicate that the Eurylaimides diversified long after fragmentation of Gondwana. Our biogeographic reconstruction identified the likely ancestral area for the Eurylaimides as Asia. A southern origin of the OW suboscines (fig. 1) and an early diversification in Asia in the Tertiary require a mechanism for transporting an ancestral lineage from the Southern to the Northern Hemisphere. The Deccan Plate (Greater India) has been implicated in transporting southern lineages to Asia (e.g., Bossuyt and Milinkovitch, 2001; Conti et al., 2002; Gower et al., 2002) and was a likely

conduit for conveying the Eurylaimides to Laurasia as well. Traditional palaeogeographic reconstructions depict India and Madagascar separating from Antarctica between 120–115 Ma (e.g., Barron, 1987; Scotese, 1991), well before our estimated date of 70 Ma for the stem of the OW suboscines. Geologists (Hay et al., 1999) as well as paleontologists and systematists (Krause et al., 1997; Buckley et al., 2000; Cracraft, 2001; Carrano et al., 2002; Case, 2002) have proposed remnant land connections between East Antarctica and Madagascar-Seychelles-India that extended into the Late Cretaceous, but none as late as 70 Ma. Thus, given current palaeogeographic evidence, over-water dispersal must be invoked to explain the split between the Old and New World suboscines. Although each of the three clades of OW suboscines contains African species, it is less parsimonious to infer an African origin (see earlier comments; tables 2, 3), and such a scenario also would require over-water dispersal.

The biogeographic history of Indian faunas around the K/T boundary is of particular interest because of India's potential role in facilitating biotic interconnections among Asia, Africa, Madagascar, and Antarctica. If India were the conduit for suboscines reaching Asia, the duration of their isolation on a drifting Greater India can be compared to that of other groups. Data from some faunal studies (e.g., frogs: Bossuyt and Milinkovitch, 2001; Caecilians: Gower et al., 2002) indicate lengthy isolation on India, resulting in high levels of endemicity and distant relationships to other taxa. In contrast, some broad surveys (e.g., Sahni, 1984; Briggs, 1989) reveal little or no evidence of prolonged isolation. Our evidence indicates this is the case also for OW suboscines: the relatively short stem lineage of the Eurylaimides (~10 Ma, fig. 4) points to a short period of isolation on India as it rafted northward in the Indian Ocean.

The Enigma of *Sapayoa*

Our results suggest that major lineages of pittas and broadbills evolved during a relatively short window of time in the Early Eocene, coincident with important geologic and climatic events in Laurasia. Northeast India made contact with the Asian continent by the Paleocene (Beck et al., 1995; Yin and Harrison, 2000), allowing pittas and broadbills to expand into Laurasia. This was the warmest time in the Tertiary, and latitudinal temperature gradients were low enough to allow tropical floras to extend up to latitudes of 50°N (Crowley and North, 1991; Frakes et al., 1992). Subtropical evergreen and seasonal forest covered the polar region, and a typically tropical fauna, including crocodilians and flying lemurs, occurred as far north as Ellesmere Island, 78°N paleolatitude (Estes and Hutchinson, 1980; McKenna, 1980). Thus, there was no impediment to tropical taxa expanding into large portions of the Eurasian continent at that time. In the mid-Tertiary, Old World suboscines apparently occurred well north of their current distribution; fossils identified as suboscine have been found from the Oligocene of France (Mourer-Chauviré, 1995) and the Miocene of Germany (Ballman, 1969), although the affinities of the Oligocene fossils have been questioned (Mayr, 2005).

The first phylogenetic event after the primary divergence of the broadbill lineages was the separation of the Neotropical genus *Sapayoa* from broadbill clade B (figs. 2, 4). To explain *Sapayoa*'s origin, Fjeldsa et al. (2003) hypothesized multiple colonizations of South America from Antarctica. Our DNA sequences and morphological data, as well as a shared deletion in Fjeldsa et al.'s (2003) intron data (see above), provide strong support for a sister relationship between *Sapayoa* and broadbill clade B (figs. 2–4). This indicates that the origin of *Sapayoa*, and the sole NW/OW split in the phylogeny, occurred *after* pittas and broadbills began diversifying. Because of this, Fjeldsa et al.'s (2003) biogeographic hypothesis also requires multiple subsequent colonization events from Antarctica to India (or Africa) in order to account for a minimum of three lineages of Eurylaimides (pittas and two broadbill clades) that existed by that time.

Our phylogeny and divergence time estimates offer an alternate explanation, namely that OW suboscines dispersed to the New World via a northern land route. Age esti-

mates suggest that *Sapayoa* diverged approximately at 52 Ma, which was after India contacted Eurasia (Beck et al., 1995; Yin and Harrison, 2000). This divergence is also congruent with the Eocene thermal maximum, high latitude tropical forests in Laurasia, and land connections to the New World. Dispersion to the New World occurred in other taxa at that time via land routes across the North Atlantic or the Bering Sea (e.g., Kvacek and Manchester, 1999; Manchester, 1999; Mourer-Chauvire, 1999; Kvacek et al., 2000; Donoghue, et al., 2001; Manos and Stanford, 2001; Xiang and Soltis, 2001; Golovneva, 2002). The North Atlantic route was severed ~52 Ma (Courtillot et al., 1999; Mosar et al., 2002), coincident with our estimate of *Sapayoa*'s divergence. Once in North America, we suggest its distribution tracked the extent of suitable habitat, which contracted southward through the Tertiary.

Fjeldsa et al. (2003) considered this explanation (dispersal across the North Atlantic or Bering Sea) implausible because of the lack of suboscine fossils in North America. Considering the sparse fossil record of passerines, and suboscines in particular, this is not surprising. The earliest fossil of the Eurylaimides is a putative broadbill from the Miocene of Europe (Ballman, 1969; Manegold et al., 2004), too recent to shed light on the origin of *Sapayoa* or other OW suboscine lineages as it has not been identified more precisely. Fossil evidence from earlier in the Tertiary or from North America (or from elsewhere in the world for that matter) is lacking, and it is unknown which gaps in the fossil record truly reflect absence as opposed to poor preservation. The age estimates and phylogenetic pattern are more consistent with a Laurasian origin of *Sapayoa* than one from Gondwana.

Origin of the Asities

The biogeographic history of the asities, a small clade restricted to Madagascar, poses a problem of timing as well as of origin. The asities are sister to a clade of African and Asian taxa, so historical processes involving both areas must be considered. A vicariance scenario among taxa on these three landmasses within the timeframe supported by our clock analysis does not appear plausible (Plummer and Belle, 1995). Prum (1993) concluded that the asities' isolation on Madagascar was due to a dispersal event from Africa, but that inference was based on a hypothesized sister relationship between the asities and *Pseudocalyptomena*. Our data do not support such a relationship; the asities are sister to a clade including *Pseudocalyptomena* and several Asian broadbills.

Date estimates for the origin of the asities (~41 Ma) and their phylogenetic position nested well inside the eurylaimid radiation are consistent with the hypothesis that the asities reached Madagascar from either Africa or Asia, and are not a relict of the Eurylaimides' Gondwanan origin. Evidence that *Sapayoa* reached the New World via North Atlantic or Beringian land bridges (see above), as well as the results from DIVA and WAAA, is consistent with the clade including *Sapayoa*, the asities, and broadbills (clade B, figs. 2, 4) having had an ancestral distribution in Asia. Hypothesizing an African origin would necessitate extra dispersal events. Madagascar lies closest to Africa, but has been separated from it by ocean barriers for 160 million years. Madagascar is currently distant from Asia, but India was much closer to Madagascar when the asities diverged in the Middle to Late Eocene. Evidence from plant distributions and the fossil record suggests stepping-stone dispersal across narrow water gaps between India and Madagascar into the Oligocene (Schatz, 1996). At ~88–84 Ma, fan-shaped spreading between India and Madagascar initiated with the opening of the Mascarene Basin, producing a narrow deep-water separation between Madagascar and Seychelles-India in the north, near the Amirante Ridge/Trough system (Plummer, 1996). A ridge jump occurred around the K/T boundary and spreading began between India and the Seychelles along the Carlsberg Ridge (Todal and Edholm, 1998). Although this spreading eventually produced ocean crust between India and the Seychelles, exposed land existed in the region of the Mascarene Plateau, Seychelles Bank, and Chagos-Laccadive Ridge that would have minimized over-water dispersal distances be-

tween India and Madagascar through the Eocene.

Africa–Asia Disjunctions

Multiple sister relationships between African and Asian clades occur in the phylogeny (fig. 6: nodes 4, 6, and 9). Our molecular-dating analysis indicates that these dispersal/vicariance events were temporally distinct, with one node each in the Eocene, Oligocene, and Miocene. It is inviting to look for similar disjunctions in other groups. For example, the recent estimated age of divergence between Asia and Africa reconstructed within the pittas (27.1–22.7 Ma) is congruent with estimates for biotic interchange between those areas in mammals (Kappelman et al., 2003) and oscine passerines (Barker et al., 2004). It is important to keep in mind, however, that the confidence intervals for the three Africa-Asia disjunctions in the Eurylaimides span a large portion of the Tertiary. Thus, although similar continental disjunctions occur in many other groups (e.g., Kappelman et al., 2003; Davis et al., 2002; Marivaux et al., 2002; Barker et al., 2004), inferring congruence across these taxa is imprecise at this point.

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APPENDIX 1

Specimens Included in the Study

Sources: American Museum of Natural History (AMNH), Academy of Natural Sciences Philadelphia (ANSP), Field Museum of Natural History (FMNH), Louisiana State University Museum of Natural Science (LSUMNS), Australian National Wildlife Collection (ANWC), Western Foundation of Vertebrate Zoology (WFVZ).

Species	Range	Source	Sample	GenBank accession numbers		
				RAG-1	RAG-2	Fib5
Ingroup						
Pitta soror	SE Asia	AMNH	12265	DQ320613	DQ320577	DQ320595
Pitta oatesi	SE Asia	AMNH	2636	DQ320612	DQ320576	DQ320596
Pitta caerulea	SE Asia	AMNH	10889	DQ320610	DQ320574	DQ320594
Pitta guajana	SE Asia	AMNH	10887	DQ320611	DQ320575	DQ320597
Pitta baudii	Borneo	ANSP	1224	DQ320615	DQ320579	DQ320593
Pitta sordida	SE Asia to New Guinea	AMNH	9633	AY443319[b]	AY443206[b]	DQ320589
Pitta erythrogaster	Philippines to New Guinea	FMNH	358341	DQ320616	DQ320580	DQ320592
Pitta angolensis	sub-Saharan Africa	FMNH	396328	DQ320619	DQ320583	none
Pitta iris	Australia	ANWC	33715	DQ320618	DQ320582	DQ320591
Pitta versicolor	Australia, New Guinea	AMNH	2371	DQ320617	DQ320581	DQ320590
Smithornis capensis	sub-Saharan Africa	LSUMNS	B21171	DQ320608	DQ320572	DQ320600
Smithornis rufolateralis	sub-Saharan Africa	AMNH	2544	AY057031[a]	AY443228[b]	none
*Pseudocalyptomena graueri**	Albertine Rift, Africa	AMNH	764296	DQ320624	none	none
*Corydon sumatranus**	SE Asia	AMNH	821833	DQ320623	none	none
*Cymbirhynchus macrorhynchos**	SE Asia	WFVZ	38303	DQ320621	none	none
Eurylaimus javanicus	SE Asia	LSUMNS	B38577	DQ320620	DQ320584	DQ320602
*Eurylaimus ochromalus**	SE Asia	WFVZ	38340	DQ320622	none	none
Serilophus lunatus	SE Asia	AMNH	12273	DQ320614	DQ320578	DQ320603
Psarisomus dalhousiae	SE Asia	AMNH	9563	AY057025[a]	AY443214[b]	none
Calyptomena viridis	SE Asia	LSUMNS	B36399	DQ320606	DQ320570	DQ320599
Calyptomena whiteheadi	Borneo	LSUMNS	B36470	DQ320607	DQ320571	DQ320598
Philepitta castanea	Madagascar	FMNH	345690	AY057018[a]	AY443201[b]	DQ320604
Neodrepanis coruscans	Madagascar	FMNH	393232	AY443306[b]	AY443181[b]	DQ320605
Sapayoa aenigma	Panama, Colombia, Ecuador	LSUMNS	B2329	DQ320609	DQ320573	DQ320601
Outgroup						
Tyrannus tyrannus		AMNH	24560	AF143739[c]	AY443243[b]	DQ320587
Furnarius rufus		AMNH	10431	AY056995[a]	AY443149[b]	DQ320588
Parus major		AMNH	10870	AY443314[b]	AY443197[b]	DQ320586
Cyanocitta cristata		AMNH	no voucher	AY443280[b]	AY443137[b]	DQ320585
Acanthisitta chloris		GenBank		AY056975[a]	AY443102[b]	none
Coracias caudata		GenBank		AF143737[c]	AY443126[b]	none

[a] Barker et al., 2002.

[b] Barker et al., 2004.

[c] Groth and Barrowclough, 1999.

* Samples for which DNA was extracted from museum study skins.

APPENDIX 2

MORPHOLOGICAL DATA SET FROM PRUM (1993) WITH EXPANDED TAXON SAMPLING

Characters 1–19 are syringeal and 20–21 are osteological. Characters 22–36 include informative morphological characters from Raikow (1987). Codes: (0) primitive state, (1) derived state, (2) alternate derived state, (?) character state unknown.

	Characters																																							
										1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3							
Taxon	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6				
Pitta species	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Smithornis species	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	2	1	1	0					
Calyptomena viridis	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	1	0	2	1	0	0				
Calyptomena whiteheadi	0	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	1	0	1	0	0	0	0	1	0	2	1	0	0				
Eurylaimus ochromalus	2	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0				
Eurylaimus javanicus	2	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?				
Cymbirhynchus macrorhynchus	2	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0				
Serilophus lunatus	2	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0				
Psarisomus dalhousiae	2	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	2	0	1	0	2	1	1	0				
Pseudocalyptomena graueri	2	1	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	2	0	0	0				
Philepitta castanea	2	1	0	1	1	0	1	0	1	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0	1				
Neodrepanis coruscans	2	1	1	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1				
Sapayoa aenigma	2	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?				
Corydon sumatranus	2	1	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?				